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OVERWINTERING EGG MASS ADAPTATIONS OF THE EASTERN TENT CATERPILLAR, *MALACOSOMA AMERICANUM* (FAB.) (LEPIDOPTERA: LASIOCAMPIDAE)[1]

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Abstract.—Experiments were designed to determine the role of the spumaline covering eastern tent caterpillar egg masses as an adaptation for overwintering. The ability of the spumaline to absorb water from the environment is a direct function of temperature and water concentration in air. Egg mass temperatures may be significantly higher than ambient temperatures. The spumaline covering egg masses of this species may act to ameliorate low overwintering temperatures and to prevent desiccation by absorbing as much moisture from surrounding air as possible.

The survival success of overwintering insects is achieved by many adaptations which overcome or compensate for extremes and fluctuations in winter conditions. In the temperate regions adaptations like the presence of cryoprotectants, low supercooling points and reduced metabolic activity (dormancy) are examples of physiological adaptations. More subtle but equally important to survival are microenvironmental adaptations, such as location of hibernacula and external protective structures.

Malacosoma americanum (Fab.), the eastern tent caterpillar, overwinters as a pharate larva inside its egg shell. Egg masses are laid on branches of suitable hosts in early summer. Complete embryonation occurs within 3–4 weeks. These mature embryos remain dormant from late July to April of the following year (Mansing, 1974). Characteristically the egg masses of all North American species (except *M. tigris*) are covered with a froth called spumaline. This material which is produced in accessory glands is deposited by the ovipositing female on top of the newly laid eggs. Very little is known about this material. Hodson and Weinman (1945) described important features of the spumaline on eggs of *Malacosoma disstria* such as its ability

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to absorb atmospheric moisture and elucidated the role of spumaline in the eclosion process.

This investigation examines, in further detail, the adaptive role of the spumaline of overwintering *Malacosoma americanum* egg masses in modulating environmental temperature and humidity.

MATERIAL AND METHODS

All tent caterpillar egg masses examined were collected from black cherry trees (*Prunus serotina* Ehrh.) located in Amherst, Massachusetts (42°23′N, 72°32′W) during the months of January–April 1979.

Hygroscopic properties of spumaline. To test water absorption capabilities of egg masses, field collected egg masses were exposed to three different temperatures: 0°C, −5°C, −10°C and five different saturation deficits per temperature for a total of 15 treatments, replicated 3 times each with 9 egg masses per replicate. Before being used in experiments any egg mass sections not covered by spumaline were covered with wax. All egg masses were placed in a controlled temperature chamber at 5°C until experiments began.

Our initial attempts to establish the hygroscopicity of the spumaline at low temperatures and high saturation deficits resulted in water loss to the surrounding environment. Therefore, subsequent experiments used desiccated egg masses, which resulted in better determination of expected water gain. Water absorption of the spumaline is expressed in terms of percent weight gain of egg mass (previously desiccated to a constant weight) maintained in humidity chambers for 24 hr. The humidity chambers consisted of closed glass containers (105 × 76 × 76 mm) where egg masses were suspended with zinc wire above a given aqueous sulphuric acid solution (Solomon, 1951). Vapor pressures for corresponding sulphuric acid solutions at temperatures ranging from 0°C to 235°C can be calculated with the aid of "International Critical Tables" (Washburn, 1928). Unfortunately, simulation of common mid-winter conditions requires creation of saturation deficits at temperatures lower than 0°C. To obtain vapor pressures for solutions below 0°C, extrapolations were made from correlations of $\log_e$ vapor pressure vs. temperature. In all correlations performed the Pearson's correlation coefficient was $r = 0.999$ ($P < 0.001$). Saturation deficits (SD) were calculated from the formula:

$$SD_t = e_s - e \qquad \text{(Rosenberg, 1974)}$$

where e_s is the saturation vapor pressure at temperature t°C and e is the actual vapor pressure, both in mm Hg.

Insulative properties of the spumaline. To determine the effect of the spumaline layer on the temperature of egg masses in the field, temperature measurements were made of egg masses on trees with a thermocouple probe

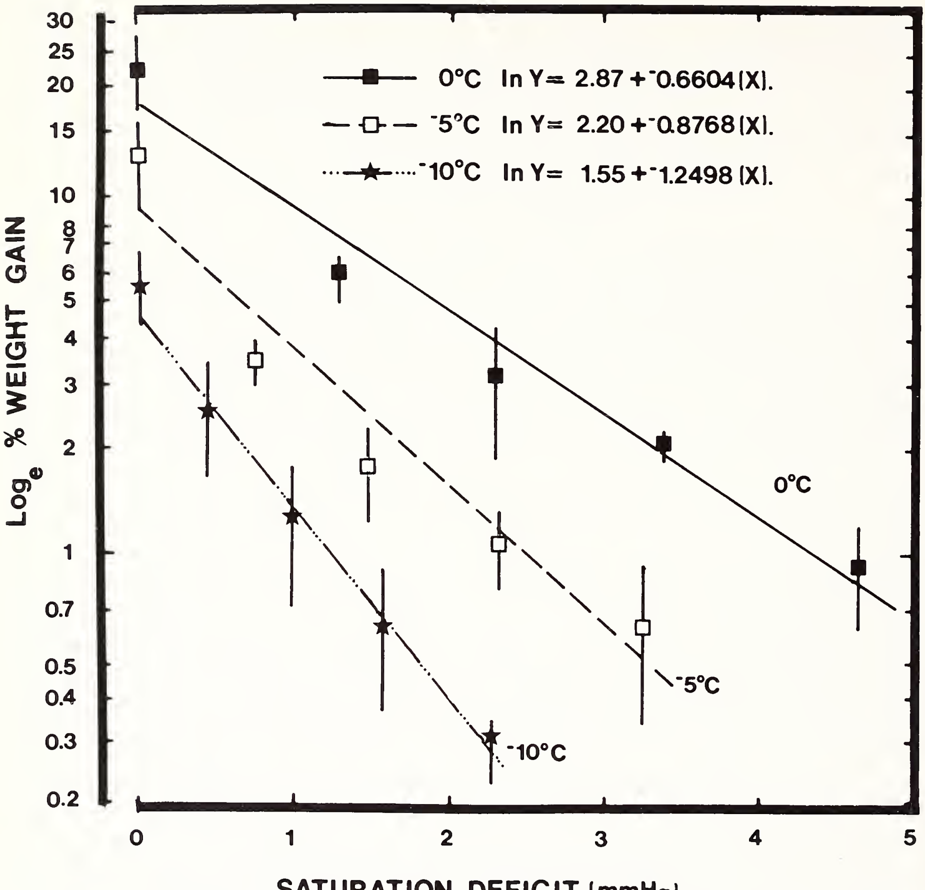

Fig. 1. Log$_e$ of percent of weight gain of *Malacosoma americanum* (Fab.) exposed to different absolute humidities −10°C, −5°C and 0°C for 24 hr (mean and SD).

and a cryothermometer model Bat-5 (Bailey Instrument Co.). For each egg mass the information recorded included type of day (e.g., cloudy or sunny), temperature inside the spumaline (but above the eggs themselves) and ambient temperature (temperatures were taken to the nearest 0.5°C).

Egg masses stored in the laboratory for two weeks at 11°C and 9.8 g/m^2 absolute humidity were utilized to study the reflectance spectrum of the chorion and spumaline. Study of reflectance spectrum is an important tool in determining how different light wavelengths behave on media and thus their energy trapping characteristics. The spectrum was measured with a Shimadzu Spectronic 210 UV Spectrophotometer equipped with an integrating sphere 200 UV attachment for measuring solid materials.

Table 1. Differences between air temperature and egg masses of *Malacosoma americanum* on clear days.

Air temperature range (°C)	Mean temperature difference: under the spumaline and air (°C)	Number of egg masses examined
9 to 5	+1.6	29
4 to 0	+2.7	47
−1 to −5	+3.0	122
−6 to −10	+3.5	73
−11 to −20	+6.0	67

RESULTS

Water absorption decreased logarithmically with increasing saturation deficit (Fig. 1), i.e., the less water in the environment the less water the spumaline absorbs at all the temperatures tested. The regression analyses of water absorption at ($r^2 = -0.99$, $P < 0.01$), −5°C ($r^2 = -0.98$, $P < 0.01$) and −10°C ($r^2 = -0.99$, $P < 0.001$), show that water absorption is a direct function of temperature and water concentration. Examination of the regression equations' slopes reveals an inverse relationship between temperature and the magnitude of the slope, furthermore, the slope of the −10°C regression line is significantly larger ($t = 3.86$, $P < 0.0005$). These two facts agree with a fundamental characteristic of hygroscopic materials where decreasing temperatures mark a corresponding increase in any material's ability to absorb water (Hodson, 1937).

Although water uptake occurs at the air-spumaline interface, it may also occur at the chorion-spumaline interface since the chorion also is hygroscopic (Hodson and Weinman, 1945; and pers. obs.). A differential response to temperature and/or humidity at each interface could account for the nonlinear nature of the water absorption curves. In addition, it was also observed that immediately after rainfall, and at temperatures higher than 10°C, field collected spumaline contains so much water that it can be literally squeezed out. This illustrates the extent of spumaline's hygroscopicity at high absolute humidity (characteristic of higher temperatures). (Also see Hodson and Weinman, 1945.)

Preliminary field measurements of temperature differences between egg masses and ambient showed that although marked temperature differences are observed on clear sunny days these disappeared during cloudy days even when measurements are taken on the same egg mass. Thus, Table 1 presents a summary of data for egg masses measured on clear days only. It was observed that differences varied inversely with environmental temperature. In some specific comparisons, egg masses were up to 12°C warmer than air

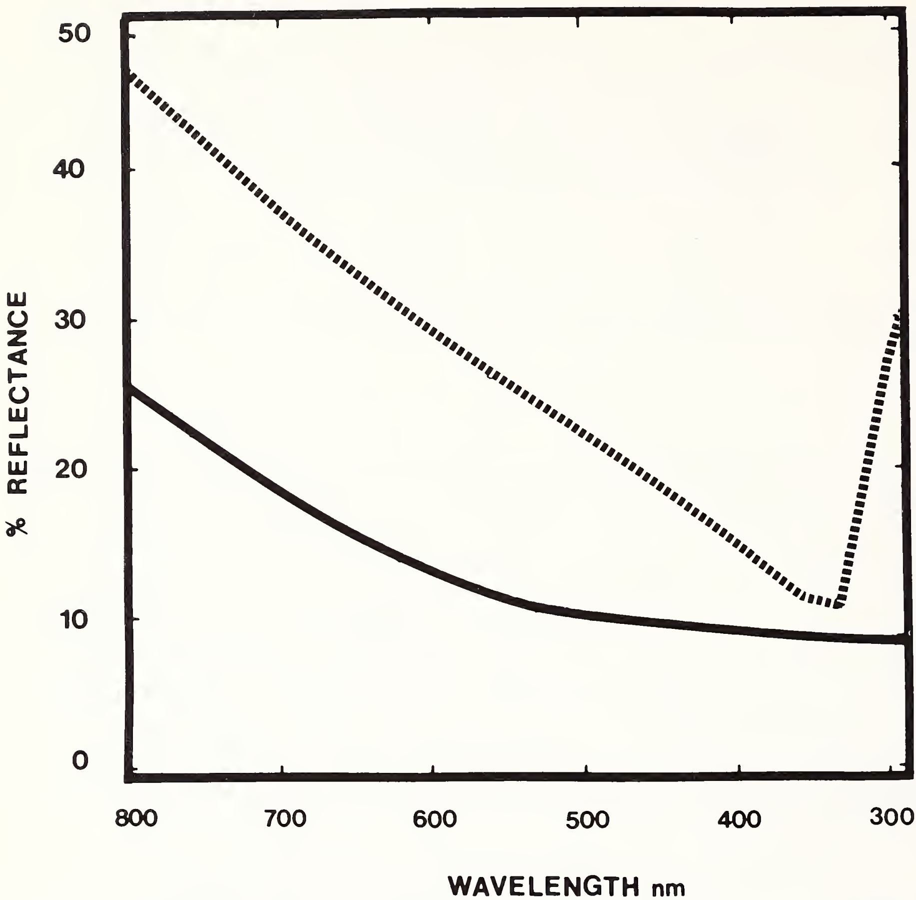

Fig. 2. Percent reflectances of the chorion (· · · · ·) and the spumaline (——) of egg masses held at 9.8 g/m^3 absolute humidity and 11°C.

temperature. These differences are in concert with differences of up to 5°C on an egg mass of *M. disstria,* during one cold and clear February day found by Wellington (1950). This observation points at the importance of solar radiation.

The reflectance spectrum of the spumaline and the chorion is presented in Figure 2. The percent reflected light decreased with decreasing wavelength with a reflectance minimum at 342 nm, in the near ultraviolet region for both structures. The fact that the spumaline consistently had high reflectance values at the infrared (IR) region of the spectrum suggests that: as short high energy wavelength radiation penetrates the chorion and spumaline some of its energy is reemitted as IR, which in turn is trapped in the spumaline, due to its large reflectivity. Thus a greenhouse effect is probably created between the chorion and the air-spumaline interface. This effect would maintain egg mass temperatures above those in the air on days when the UV component of incident light is large (i.e., on sunny clear days).

DISCUSSION

The hibernacula of many insects occur under or within snow cover, bark, leaf litter or soil. These substrates provide relatively small temperature fluctuations and excellent insulative qualities (Holmquist, 1931). On the other hand, the overwintering stage of *Malacosoma americanum* in its arboreal habitat is exposed to wide environmental fluctuations and low temperatures. Under these conditions, species like those of *Malacosoma* tend to have cold-hardy overwintering stages (MacPhee, 1964). Several physiological mechanisms of cold-hardiness in *Malacosoma* have been reported namely the presence of high cryoprotectant levels and low supercooling points (Hanec, 1966; Mansingh, 1974). However, although important these are not the only ways to compensate for climatic extremes. The egg masses of many overwintering arthropods are often protected from cold environments by materials provided by the maternal parent. The eggs of the gypsy moth can withstand temperatures of −50°C if the masses are covered by the hair placed on them by the female, but die at −19°C if the hairs are removed (Kulagin, 1897, cited in Danks, 1978). Similarly, the egg sac of *Floridia bucculenta* protects eggs from desiccation and flooding (Schaefer, 1976). In *Malacosoma* the presence of the spumaline appears to serve two purposes: to ameliorate environmental temperatures and to prevent desiccation. The spumaline insures the capture of the water when the humidity is high and serves as an interphase for slow evaporation when air moisture is low. Extremely dry winters seldom occur in the natural range of *M. americanum* where precipitation is usually high. The suggestion of Hodson and Weinman (1945) that the spumaline of *M. disstria* was essential for its winter survival appears to apply equally well to *M. americanum*.

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